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THE FERTILIZATION OF SALVIA SPLENDENS BY BIRDS.[1]

BY WILLIAM TRELEASE.

IN the fall of 1878, while studying the structure of various flowers, as correlated with the mode of their fertilization, I examined *Salvia splendens* Sellow,[2] a Brazilian species very commonly cultivated for its large scarlet flowers. From the structure as then made out, I was partially convinced that I was not dealing with an entomophilous flower; but it was not until two years later that I had an opportunity to look into the matter any further, and I then became certain that the species was one of the more closely adapted ornithophilous plants.

The flowers, arranged in a compound raceme, are placed horizontally or nearly so. Nectar, secreted by a large, lobed disk (*n*), as usual in the Labiatæ, accumulates in the basal part of the corolla, and offers a considerable amount of tempting food to nectar-loving creatures, and this, advertised by the brilliant scarlet of the calyx and corolla, clearly proclaims the flowers to be zoöphilous, or adapted to fertilization by animals of some kind.

The corolla is tubular, though somewhat laterally compressed, and reaches a length of not far from two inches. It possesses the bilabiate character which has given a name to the natural

[1] Read before the Boston Society of Natural History, Feb. 2, 1881.

[2] Professor F. Hildebrand, in his paper on the fertilization of Salvias by insects (Pringsheim's Jahrb. wiss. Bot., 1865, IV, p. 459, and Pl. 33, figs. 8 and 9), describes and figures the floral structure of a species to which he gives this name, but which is quite different from that on which my observations were made, which, it may be added, has been found to agree with authentic specimens of *S. splendens* in the Gray Herbarium.

order to which it belongs, and, as is generally the case with labiate flowers, the lower lip is split into three lobes, a median and two lateral, which in this case are of nearly equal size. Here, however, the lower lip—usually well developed and affording a convenient landing place for insects—is small and of little or no use for this purpose.

The style is exserted to a considerable distance, and the included portion is held quite firmly in a longitudinal fold of the upper part of the corolla tube. The forked stigma (*st*) is thus maintained in the median plane of the flower.

The stamens are two in number, and of the general form found in this genus. Their filaments are adherent to the corolla to within a short distance of its mouth, where they become free, and run obliquely upward and forward, terminating side by side, close beneath the base of the upper lip. The connective which in many flowers forms an inconspicuous band between the anther cells, is here prolonged, in each stamen, into a slender longitudinally-placed rod nearly an inch in length. Each connective (*c*) is attached at its middle by a hinge joint to the end of its filament, thus forming an oblique lever with equal arms, which lies with its anterior end *a* in contact with, or barely protruding from the tip of the arched upper lip of the corolla, while its posterior end *a'* nearly reaches the floor of the tube. If this were constructed as the stamens of related plants are, it should bear an anther cell at each end; but in reality only a single fertile cell—the anterior—is developed, the posterior cell being abortive. Moreover, the connectives of the two stamens are coherent for a short distance back of their insertion, so that the two form, in reality, a single forked lever.

When a flower first opens, the stigma is immature, its lobes being closely appressed, as shown in the upper part of Fig. 2, but the anthers are already dehiscent. In other words the species is proterandrous. Later, when some or all of the pollen has been removed, the stigmatic lobes expand, as shown in the lower part of Fig. 2, and expose the now receptive surfaces, and the style curves down into the position shown by the dotted line of Fig. 1. From my observations, I should say that the life of a given flower may be divided into three periods; in the first, the anthers only being mature, it is staminate in function; in the second, some pollen remaining in the anthers, while the stigmas

become receptive, it is functionally hermaphrodite or perfect; and in the third, the pollen having been entirely removed, while the

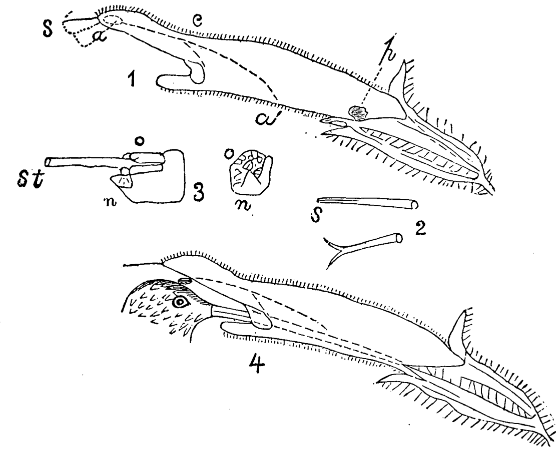

FIG. 1.—Young flower of *Salvia splendens*, seen from the side. The position of the connective and filament is shown by dotted lines, as also the position assumed by the style in older flowers. FIG. 2.—Stigmas; the upper from a newly expanded flower, the lower from a flower which has been open for some time. FIG. 3.—The nectar gland and ovary. FIG. 4.—A flower visited by a humming bird; Figs. 1 and 4 natural size; Figs. 2 and 3, enlarged four diameters; *a*, indicates the fertile anther cells; *a'*, the sterile cells; *c*, the connective, at the point where it is hinged to the filament; *n*, the nectar gland; *o*, the ovary; *p*, a perforation of the corolla, made by ants for access to the nectar; *s*, the stigma; *st*, the style.

stigma, if unfertilized, retains its freshness, it is pistillate only so far as function is concerned.

It appears at once that there is little likelihood of pollen reaching the stigma without some sort of assistance, and the proterandry decreases the chances for a given flower to be fertilized by its own pollen when such assistance is rendered, though from the apparent incompleteness of the dichogamy this may occur in some instances.

Many species of Salvia are perfectly adapted to profit by the visits of bees, usually humble bees, which, in entering the flower for nectar, encounter and elevate the posterior end of the connectives with their heads, thus bringing the polliniferous anterior end upon their backs and dusting them with pollen, which will be brushed off, in part, by the stigma of the next older flower visited. When the insect leaves the flower, the stamens, returning to their former position through the elasticity of the parts, are ready to make their bow to the next comer. Two facts, however, argue against the adaptation of the present species to bees:

1. The narrow and elongated tubular form of the corolla quite effectually excludes those which are large enough to set the lever in motion; 2. If such an insect, for instance a hive bee or small humble bee, should force its way into the tube, by the time its head had reached and elevated the sterile end of the lever, the tip of its abdomen would have passed the lowering polliniferous end, so that no pollen would reach the insect, and the object of the motion would be defeated. Bees might, to be sure, visit the flowers solely for their pollen, and I have no doubt that they occasionally do so, in which case they must often render some service in their fertilization, as is the case in so many flowers visited for pollen alone. Bees being excluded for the reasons above given, we turn to Lepidoptera, which sometimes visit the flowers, their long and slender proboscides enabling them to reach the nectar with little exertion; but it remains to be shown that these organs are sufficiently large or rigid to set the stamens in motion. Even if it should be shown that the large nocturnal moths do move the levers, which I am far from believing to be the case, the brilliant scarlet color is one ill adapted to rendering the flowers conspicuous in the twilight or night, and, so far as I know, one which is never possessed by flowers especially dependent upon these insects for their fertilization; beside which, we do not find that close constriction of the mouth or anterior part of the corolla bespeaking adaptation to the Lepidoptera. It appears, then, that when these insects visit the flowers of our sage, they may be of some use in transferring pollen, since their heads may encounter stigma and anthers, but they do this without rendering the motility of the latter of any value.

The only alternative, then, is birds, which, to be of the highest use in this connection, must be found in the native habitat of the plant, must visit flowers frequently for nectar, small insects attracted by the latter, or for both, and finally, must have slender and elongated beaks capable of insertion into the tubular flowers. All of these conditions are fulfilled by many of the humming birds, which reach their greatest number in both species and individuals in Equatorial America. The color of this Salvia is one of the most attractive to humming birds, and a glance at Figure 4 will show that one of those with an elongated beak cannot fail to operate the lever in the most perfect manner; its extensible tongue, however, rendering it by no means necessary for its beak to equal the corolla in length.

In a brief note published in the *Botanische Zeitung* for 1870, p. 275, Fritz Müller states that in Brazil the scarlet Salvias are frequently visited by birds, and although no species are named, there is little reason to doubt that the one under consideration was among those observed. Our single species of Trochilus, the ruby throat, possesses a beak rather short for the most efficient working of the staminal lever, yet from the statements of friends and from personal observation I can vouch for its frequently rendered service, and the greater part of the capsules of this plant which mature in our borders are to be credited to this active little creature.

Although this paper is confined to a single species of Salvia, it by no means follows that others may not offer examples of equal or even of greater adaptation to birds, and several such might be mentioned. The conclusion seems, on the whole, warranted, that several tropical American Salvias are as perfectly adapted to profit by the visits of birds as many other species of the genus are to profit by the visits of bees.

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ON THE ORIGIN OF THE FOOT STRUCTURES OF THE UNGULATES.

BY E. D. COPE.

THE following considerations have been suggested by a study of the primitive types of the odd and even-toed ungulates. I first, in 1874, recorded the opinion that the *Mammalia* with a reduced number of digits were derived from pentadactyle plantigrade types.[1] The ungulate order which fulfills this requirement is the *Amblypoda*, and from them, I doubt not, both the *Perissodactyla* and *Artiodactyla* have arisen, although not from any of the genera now known. Both of these great orders display a regular diminution in the number of the digits; in the former, by reduction and extinction on both sides of the third digit; in the latter, by reduction and extinction on each side of the third and fourth digits. Mr. John A. Ryder[2] has pointed out that reduction in digits is probably directly related to strains and impacts. He reminds us that the anterior digits are reduced in *Mammalia* of unusual scansorial or fossorial powers; while in forms which display

[1] Journal Academy Philadelphia, March, 1874.

[2] AMERICAN NATURALIST, October, 1877.